Ecological Modelling 325 (2016) 47–56

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Response of semi-arid savanna vegetation composition towards grazing along a precipitation gradient—The effect of including plant heterogeneity into an ecohydrological savanna model

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ARTICLE INFO

Article history:
Received 18 September 2015
Received in revised form
21 December 2015
Accepted 7 January 2016
Available online 5 February 2016

Keywords:
Plant functional types
Trait heterogeneity
Rangeland management
Precipitation gradient
Livestock
Ecosystem functioning

ABSTRACT

(1) Ecohydrological models of savanna rangeland systems typically aggregate plant species to very broad plant functional types (PFTs), which are characterized by their trait combinations. However, neglecting trait variability within modelled PFTs may hamper our ability to understand the effects of climate or land use change on vegetation composition and thus on ecosystem processes.
(2) In this study we extended and parameterized the ecohydrological savanna model EcoHyD, which originally considered only three broad PFTs (perennial grasses, annuals and shrubs). We defined several sub-types of perennial grasses (sub-PFTs) to assess the effect of environmental conditions on vegetation composition and ecosystem functioning. These perennial sub-PFTs are defined by altering distinct trait values based on a trade-off approach for (i) the longevity of plants and (ii) grazing-resistance.
(3) We find that increasing grazing intensity leads to a dominance of the fast-growing and short-lived perennial grass type as well as a dominance of the poorly palatable grass type. Increasing precipitation dampens the magnitude of grazing-induced shifts between perennial grass types. The diversification of perennial grass PFTs generally increases the total perennial grass cover and ecosystem water use efficiency, but does not protect the community from shrub encroachment.
(4) We thus demonstrate that including trait heterogeneity into ecosystem models will allow for an improved representation of ecosystem responses to environmental change in savannas. This will help to better assess how ecosystem functions might be impacted under future conditions.

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1. Introduction

The vegetation structure of semi-arid savannas is generally characterized by a combination of dominant perennial grasses and interspersed woody plants (Scholes and Archer, 1997). The actual abundance of single species or functional groups is thereby driven by a set of environmental factors and land use such as precipitation or grazing (Germino and Reinhardt, 2014; Hanke et al., 2014). Any change in the magnitude of those variables may thus alter ecosystem structure. Increased grazing pressure and rainfall amounts as well as combinations thereof can lead to a complete replacement of the perennial grass matrix by woody plants – referred to as shrub encroachment – or annual grasses (Skarpe, 1991; Sankaran et al., 2005). This structural change, which is often associated with degradation, can lead to severe changes in the functioning of savannas and the provision of important ecosystem services such as livestock production, water retention and tourism (Sharp and Whittaker, 2003; Ravi and D'Odorico, 2009).

To better understand the mechanisms behind degradation but also to assess its impact on ecosystem functions and services, several empirical studies analyzed the trait diversity within plant communities in semi-arid or arid systems and its response to environmental change (Frenette-Dussault et al., 2013; Hartnett et al., 2013; Laliberte et al., 2013). In this context, it has proven helpful to study the impact of climatic and land use change on plant

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http://dx.doi.org/10.1016/j.ecolmodel.2016.01.004
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functional types (PFTs) grouped by characteristic traits instead of single species (Skarpe, 1996; Weiss et al., 2014).

In savanna systems, this grouping into PFTs has been very broad in the past, and usually distinguishes only two to three general meta-plant functional types (meta-PFTs), namely woody plants, perennial grasses, and annual grasses (Blaum et al., 2009; Wasiolka et al., 2010). Also various studies addressing degradation dynamics of savannas only consider these broad meta-PFTs, although for example shifts from edible to unpalatable perennial grasses, i.e. changes of traits within one meta-PFT play a major role in degradation dynamics and this can have major implications for ecosystem functions and services (Dougill and Thomas, 2004; Klintenberg and Verlinden, 2008). However, the contribution of different sub-PFTs or trait-based strategies within the typical and common meta-PFT to vegetation dynamics and structure is usually ignored.

The focus on broader meta-PFT classification schemes is similarly apparent in savanna ecosystem models. Many available savanna models from the last decades focus on the coexistence between the meta-PFTs and how this is affected by environmental conditions. However, these models neglect potential changes in PFT composition due to climate or land use dynamics below the meta-PFT level (e.g. Jeltsch et al., 1999; Daly et al., 2000; Williams and Albertson, 2005; Wiegand et al., 2006; but see for example Beckage et al., 2009 for a savanna model on the partitioning of the meta-PFT "tree" into savanna and forest trees). Meta-PFT based approaches generally assume that trait variability within PFTs can be neglected compared to the trait variability between different PFTs. Yet, simulation results and empirical evidence from other dryland or grassland ecosystems suggest that trait variability within PFTs may help explain variations in ecosystem functioning on different scales (Schumacher and Roscher, 2009; Flynn et al., 2011; Weiss et al., 2014). This is also supported by several experimental studies, which determined trait gradients within vegetation communities (Diaz et al., 2004; Pierce et al., 2014), and the effect of trait gradients on community response to drought stress (Couso and Fernandez, 2012). Couso and Fernandez (2012) found that greater trait variability enhances the drought resistance of perennial grass species in dryland systems. Modellers of vegetation dynamics are gradually recognizing the limitations of the presently used coarse PFT definitions (Pavlick et al., 2013; Scheiter et al., 2013; van Bodegom et al., 2014), as well as the necessity to connect traits to environmental factors (Verheijen et al., 2013).

From a theoretical point of view, varying traits may hint at trade-offs within a given plant functional type (Reich, 2014). A trade-off is hereby defined as an evolutionary game between different plant strategies where increased fitness caused by one plant trait inevitably implicates the sacrifice of fitness induced by another plant trait. The potential trade-offs are generally related to important biological activities, e.g. resource capture, nutrition storage and stress tolerance (Grime, 2001). In semi-arid systems, safety-efficiency trade-offs within a PFT maximize the resource utilization while minimizing the effects of environmental stress (Caylor et al., 2009; Manzoni et al., 2013). An experiment conducted by Busso et al. (2001) indicates that nutrient uptake rates are greater for the less grazing tolerant perennial grasses in a semi-arid savanna. This implies a trade-off between nutrient exploitation (and consequently growth rate) and herbivory tolerance within perennial grass species.

Refining broad meta-PFTs into sub-PFTs that are given by a spectrum of trait-based trade-off mechanisms might be one way to improve the limitations of current savanna models. Importantly, neglecting trait-based trade-offs when modelling vegetation dynamics may cause the occurrence of 'Jack-of-all-traders' which would ultimately lead to contradictions with ecological reality (Pichancourt and van Klinken, 2012). Defining low-dimensional trade-offs (between two plant traits) provides a promising starting point to describe plant composition and to explicitly describe trait heterogeneity (Esther et al., 2011). Trait selection should ideally focus on specific traits that reflect the plant's response to environmental stressors, and thus help to understand the impact of trait diversity on ecosystem stability (Loreau and de Mazancourt, 2013). Simultaneously, trait selection should consider the feasibility of measuring traits in field campaigns to increase the comparability to prior studies, as well as possess indicative capacity on ecosystem functions (Pillar, 1999).

In this study, we extended the eco-hydrological savanna model EcoHyD (Tietjen et al., 2009, 2010; Lohmann et al., 2012; Tietjen, in press) to analyse the effects of trait variation within meta-PFTs on vegetation dynamics and ecosystem stability with respect to degradation under a broad range of land use and precipitation scenarios. The model was technically prepared to include various sub-PFTs instead of being restricted to three meta-PFTs. Subsequently, trait heterogeneity within the perennial grass meta-PFT was incorporated into the model, by implementing trade-offs between contrasting traits, namely growth vs. mortality and grazing-resistance vs. (re-)growth. We applied the extended model to analyze the following two questions:

(1) How do mean annual precipitation and grazing intensity influence the long term dynamics of perennial sub-PFTs?
(2) How does the increased trait heterogeneity in the model affect ecosystem functioning (here the total vegetation cover and water use efficiency) of the simulated system?

2. Methods

2.1. Model description

This study is based on the ecohydrological savanna model EcoHyD (Tietjen et al., 2009, 2010; Lohmann et al., 2012). EcoHyD divides the landscape into grid cells with a resolution of 5 m by 5 m. The model is composed of a hydrological sub-model (Tietjen et al., 2009) and a vegetation sub-model (Tietjen et al., 2010; Lohmann et al., 2012). In the vegetation sub-model, demographic processes including growth, mortality, dispersal, establishment, competition for water and space of three plant functional types (PFTs: shrubs, perennial grasses and annual grasses) and grazing by livestock are simulated in biweekly to annual time-steps. Although fire has been found to be important for the system with regard to the early life-stages of the woody plant type (Joubert et al., 2012; Lohmann et al., 2014), we did not explicitly include fire in this model version as we rather focus on the dynamics of the perennial grass type here. The latter was found to be relatively resistant towards the effect of fires on larger spatio-temporal scales (Zimmermann et al., 2010). In addition, in our study we focus on a managed semi-arid savanna system, in which fires are usually suppressed directly by land users, and indirectly via reduced grass fuel biomass. In the underlying hydrological sub-model soil water dynamics including infiltration and runoff, water fluxes between two soil layers as well as evapotranspiration, are calculated in an hourly to daily resolution. The simulations for this study were carried out on 30 by 30 grid cells and for a total time period of 200 years. The main model and its equations are described in previous publications (hydrological sub-model: Tietjen et al., 2009; vegetation sub-model: Tietjen et al., 2010; Lohmann et al., 2012). Here we focus on model changes that were made to address the questions posed in this study (a full model description and a conceptual figure of the processes can be found in Appendix A (Fig. A1)). The original model was extended with respect to two main features: (i) evapotranspiration was separated into evaporation and transpiration and (ii) the perennial grass PFT was sub-classified to account for variability within this PFT.

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